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DIGESTIVE ENZYMES OF AN INSECT.*

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INTRODUCTION.

Digestion is a phase of Insect Physiology on which surprisingly little research has been done, considering the economic importance of the food of insects and the fact that our most important control measures involve the action of digestive juices on poisons taken into the digestive tract.

The cockroach (*Blatta orientalis* Linn.) was chosen for this study as it was available in quantities, and represented a generalized type of insect. Methods found of value in its study can be readily used upon such specialized types as the wood-, meat-, starch-, and sugar-feeders.

Our little knowledge of this problem is due to the investigations of F. Plateau (1), carried on about 1875. He came to the following conclusions:

1. The saliva of the cockroach changes starch to glucose, and is either neutral or alkaline. The reduction of copper in Barreswil's solution, a reagent similar to Fehling's solution, was taken as an indication of the presence of glucose.

2. The fore gut does not secrete digestive fluids. The contents are neutral, alkaline, or acid, depending on the food eaten.

3. The gastric cœca secrete a fluid which digests proteins. In his paper, "Les phenomenes de la digestion chez la Blatte americaine," he reports the fluid alkaline. Miall and Denny (2), cite him as having found it acid.

4. In the mid gut proteins are digested and fats emulsified(1). Miall and Denny (2) report Plateau in 1886 as having believed that no digestion takes place there.

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In the first series of tests in the present work, tissue suspensions were used, while in the second series the canal contents were tested directly. Macrochemical enzyme tests were used in the first case, and microchemical methods were developed for use in the second series.

I wish to acknowledge my great indebtedness to Drs. J. F. Lyman, C. H. Kennedy and R. C. Osburn, Ohio State University, for criticisms and suggestions.

Macrochemical Tissue-Suspension Method.

Tissue suspensions of the various organs were prepared and the presence of the enzymes tested for. An equal number of checks and tests were run for each experiment. The checks were made up in exactly the same manner as the tests, except that the tissue suspensions were first boiled to destroy the enzymes.

Preparation of the Tissue-Suspensions.

Insects, freshly killed with chloroform, were dissected under distilled water. The digestive tracts were removed, split open, and the contents thoroughly washed out, using distilled water. Each tract was then divided into the following four parts: fore gut, gastric cœca, mid gut, and hind gut. The salivary glands were also removed, and each of the tissues placed in a separate flask containing 30 cc. of pure glycerin.

After these tissues had been secured from 100 roaches, the glycerin-whole tissue suspensions were poured into mortars and the tissues reduced to a pulp with a pestle. The resulting suspensions were then replaced in the flasks and were ready for use. They will keep indefinitely.

AMYLASE.

This enzyme hydrolyzes starch, forming maltose.

Davis' Potato Starch Substrate (6): Add 10g potato starch to 250 cc. water. Boil with constant stirring till opalescent. Transfer to a 2 liter flask containing 500 cc. boiling water. Boil under reflux condenser for two hours. Cool, and make up to 1 liter. Preserve with 2% toluene.

Procedure: To 5 cc. of the above solution, add 1 cc. tissue suspension and .5 cc. toluene.

Iodine Test: Test every two minutes with iodine solution for the presence of starch. Record time taken to reach achromic point.

Fehling's test: After 48 hours, the above solution was tested for the presence of reducing sugars with Fehling's solution.

Results: Salivary gland.....heavy precipitate.
Other tissues and checks.....no precipitate.

Conclusion: Amylase is present only in the salivary gland.

MALTASE.

This enzyme hydrolyzes maltose, forming glucose.

Procedure: 35 cc. of 1% maltose solution plus 1 cc. tissue suspension plus 2 cc. toluene. Incubate 24 hours at room temperature.

Barfoed's test for monosaccharides:

Salivary gland	no precipitate.
Fore gut	slight "
Gastric cœca	heavy "
Mid gut	heavy "
Hind gut	no "
5 checks	no "

Saccharimeter Readings (Bates' type instrument):

Tissue	18 hours	22 hours
Salivary glands	+6.1	+6.1
Check	+6.1	+6.1
Fore gut	+5.5	+5.4
Check	+6.1	+6.1
Gastric cœca	+4.5	+4.1
Check	+6.1	+6.1
Mid gut	+5.5	+5.0
Check	+6.1	+6.1
Hind gut	+6.2	+6.2
Check	+6.2	+6.2

Conclusion: Maltase is present in the foregut, gastric cœca, and mid gut.

INVERTASE.

This enzyme hydrolyzes sucrose, forming fructose and glucose.

Procedure: 5 cc. of 1% sucrose solution + 1 cc. tissue suspension + .5 cc. toluene. Incubate 18–24 hours at room temperature.

Fehling's test for reducing sugars:

Salivary gland	no precipitate
Foregut	slight "
Gastric cœca	heavy "
Mid gut	heavy "
Hind gut	no "
5 checks	no "

Conclusion: Invertase occurs in the fore gut, gastric cœca, and mid gut.

Results: Salivary gland, 20 minutes. Other tissues and checks showed no digestion in 48 hours.

LACTASE.

This enzyme hydrolyzes lactose, forming glucose and galactose.

Procedure: 5 cc. of 1% lactose solution + 2 cc. tissue suspension+2 cc. toluene. Incubate 24 hours at room temperature.

Saccharimeter Readings (Bates' Type Instrument):

Salivary gland	+3.00
Check	+3.00
Fore gut	+3.00
Check	+3.00
Gastric cœca	+3.00
Check	+3.00
Mid gut	+3.00
Check	+3.00
Hind gut	+3.00
Check	+3.00

Conclusion: Lactase is not present.

LIPASE.

This enzyme splits fats into fatty acids and glycerol.

Bloor-Raper (6, 9) *Neutral Olive Oil Emulsion:*

To 4 g. of casein, on a water bath, add water till a thin paste is formed Add two drops of phenolphthalein and enough N/1 NaOH to give a permanent pink tinge. Stir in 8 cc. olive oil till the globules disappear. Cool, dilute to a 4% emulsion.

Procedure: 5 cc. emulsion+2 cc. tissue suspension +.5 cc. toluene. Incubate 18 hours at room temperature. Titrate the freed acid with N/20 NaOH. Phenolphthalein indicator.

Tissue	Cc. N/20 Acid present
Salivary gland	.3cc.
Check	.3cc.
Fore gut	.9cc.
Check	.3cc.
Gastric cœca	1.3cc.
Check	.4cc.
Mid gut	1.0cc.
Check	.3cc.
Hind gut	.4cc.
Check	.4cc.

This experiment was repeated with the same results, using a 2% Acacia-Olive Oil emulsion (5) with thymol as a preservative.

Conclusion: Lipase is present in the fore gut, gastric cœca, and mid gut.

PEPSIN.

This enzyme, in an acid solution, breaks complex proteins down into peptones. Fibrin, at the suggestion of Dr. Lyman, was dyed in a 1% aqueous solution of amaranth red for 15 minutes. All surplus stain was then removed by thoroughly washing with water whose acidity was adjusted to pH = 3 with HCL. This gave a red fibrin whose color would not come out in an acid solution.

Even the slightest digestion of the fibrin is then made apparent by a noticeable red color in the digested fluid.

Procedure: Adjust the tissue suspensions to an acidity whose pH=2 with HCL. 2 cc. tissue suspensions +colored fibrin+.5 cc. toluene.

Incubate 96 hours at room temperature.

No digestion was apparent.

Conclusion: Pepsin is not present in this insect.

TRYPSIN.

This enzyme, in an alkaline solution, breaks complex proteins down into peptones.

Procedure: The tissue suspensions were adjusted to an acidity whose pH=7.4 with $Na_2 CO_3$.

2 cc. tissue suspension +fibrin +.5 cc. toluene.

Gastric cœca.....digestion complete in 24 hours.

Mid gut.....digestion complete in 48 hours.

Other tissues and checks.....no digestion in 96 hours.

Conclusion: Trypsin is present in the gastric cœca and mid gut.

EREPSIN.

This enzyme splits peptones into amino-acids.

Salaskin's Phosphotungstic Acid Method (4, 3): To 25 cc. of a 1% peptone solution, whose acidity was adjusted to pH=7.6, add 2 cc. enzyme solution and 2 cc. toluene. Incubate at room temperature for 48 hours. Add phosphotungstic acid till no further precipitation occurs. Filter, and determine the nitrogen content of the precipitate by the Kjeldahl method. The presence of erepsin is indicated by a decrease in the N-content of the precipitate from that in the checks.

Tissue	g. Peptone-N(Precipitate)	Digested Peptone N.
Salivary gland	.01036g	0.0000g
Check	.01036g	0.0000g
Fore gut	.01050g	0.0000g
Check	.01050g	0.0000g
Gastric cœca	.00196g	0.0854g
Check	.01050g	0.0000g
Mid gut	.00826g	0.0124g
Check	.01050g	0.0000g
Hind gut	.01050g	0.0000g
Check	.01050g	0.0000g

Conclusion: Erepsin is present in the gastric cœca and mid gut.

Summary of Macrochemical Tissue Suspension Method.

Enzyme	Where Found
Amylase	Salivary gland.
Maltase	Fore gut, gastric cœca, mid gut.
Invertase	Fore gut, gastric cœca, mid gut.
Lactase	Absent.
Lipase	Fore gut, gastric cœca, mid gut.
Pepsin	Absent.
Trypsin	Gastric cœca, mid gut.
Erepsin	Gastric cœca, mid gut.

Microchemical Method of Enzyme Analysis.

The tissue suspension method used above is open to the criticism that it merely demonstrates the presence of enzymes in the tissues. It does not prove that these enzymes are secreted into the digestive canal nor that they function in the portion of the canal where they are secreted. Therefore, to check the above results, the contents of the various parts of the canal were collected and tested for the presence of those enzymes which had been found by the tissue suspension method.

In this investigation tests were sought which would be of use with smaller amounts of material, since the macrochemical tissue suspension method used above can find only limited application due to the large numbers of insects required for analysis.

By the following microchemical methods, the complete enzyme analysis of the canal contents can be carried out, with definite results, using the material obtained from two roaches. These tests can also be used with little or no change in tissue suspension analyses, although they were not so used in this investigation.

General Procedure.

The alimentary canals were obtained from freshly killed roaches, divided into the fore, mid and hind guts, and the contents removed. These materials were then diluted with equal volumes of distilled water, and the acidity regulated as desired. They were then ready for use.

The incubations were carried on at room temperature in micro-tubes, about 1¼ inches long, made from ¼-inch glass tubing.

The checks were made up with boiled enzyme solutions.

To each check and test, in the micro-tubes, was added enough toluene to cover the surface of the liquid. This prevents the action of microorganisms.

AMYLASE.

Starch-Iodine Test: To a dilute starch paste, add sufficient I-KI solution to give a dark blue color. Place in micro tubes, add a small amount of the enzyme solution, and cover with toluene. Incubate 48 hours. When the starch is digested, the solution will be colorless. Then, to the colorless tubes add several drops of I-KI solution. If no blue color develops, digestion is complete. This last check should be made to make sure that the loss of color was not due to the absorption of iodine by fats in the enzyme solution.

Fluckiger test for reducing sugars (12:) Incubate starch paste+enzyme solution+toluene for 48 hours. Add one drop of the resulting solution to a drop of Fluckiger's reagent on a slide. Add a cover glass and heat gently. A red precipitate of copper indicates the presence of reducing sugars.

Fluckiger's reagent: Mix a drop of 20% NaOH with an equal amount of powdered copper tartrate on a slide till the copper is dissolved. The reagent is then ready for use.

Results: Amylase was found in the fore gut, mid gut and hind gut.

MALTASE.

Procedure: 5% Maltose solution+enzyme solution+toluene. Incubate 72 hours in micro tubes.

Phenylhydrazine-Osazone Test (10): Mix one drop of Phenylhydrazine-HCL (1-10 glycerin) and one drop of Sodium acetate (1-10 in glycerin) on a slide. Add one drop of the incubated solution. Add the cover glass.

Heat on the water bath for 15 minutes. The glucose osazone will appear within an hour on cooling. Maltose osazones appear 3–4 days later.

Results: Maltase was present in the fore and mid guts.

INVERTASE.

Procedure: 5% sucrose solution+enzyme solution+toluene. Incubate 48–72 hours.

Phenylhydrazine-Osazone test: (10): This test is given above. Heat 15 minutes on the boiling water bath. Fructose osazones appear immediately; Glucose osazones within an hour on cooling.

Fluckiger test for reducing sugars: Fructose reduces the copper instantly in the cold. Glucose reduces it on warming.

Methyl-phenylhydrazine-Osazone test: Mix 1 drop of Methylphenylhydrazine acetate (1-10) in glycerin and 1 drop of sodium acetate (1-10 in 50% glycerin). Add sugar solution. Gives osazone with fructose on heating gently for 7–8 minutes.

Results: Invertase was present in the fore gut, mid gut and hind gut.

LACTASE.

Procedure: 5% Lactose solution+enzyme solution+toluene. Incubate in micro tubes 48–72 hours.

Phenyl-hydrazine-Osazone test (12): This test is described above. Glucose osazones are taken as an indication of the presence of lactase.

Results: No lactase was present.

LIPASE.

B. T. B.-Tristearin test: Wash commercial tristearin repeatedly with 70% alcohol to rid of free fatty acids. Melt, and add sufficient KOH to give it an acidity whose pH = 7.2. Pour into the micro tubes to a depth of ½ inch. Allow to harden.

Add several drops of Brom Thymol Blue to the enzyme solution and sufficient $Na_2 CO_3$ to give it a blue color (pH = 7.2).

Add the blue enzyme solution to the tristearate in the micro tubes, cover with toluene, and incubate 48–96 hours.

As the fat is digested a green to yellow zone forms at the junction of the fat and liquid, and eventually the entire solution becomes greenish yellow to yellow due to the liberation of fatty acids.

B. T. B.-Emulsion test: Add several drops of Brom Thymol Blue to the emulsions prepared as directed under the tissue suspension method for lipase. Add sufficient NaOH to give a blue color. Prepare the enzyme solution as in the above test and add it to the blue emulsion in micro tubes. Incubate 48–96 hours.

The change from blue to greenish yellow or yellow indicates the presence of lipase.

Results: Lipase was present in the fore gut and mid gut.

PEPSIN.

Colored Fibrin method: Color fibrin with Amaranth red as directed under the tissue suspension method for Pepsin. Place a small piece of the red fibrin in the bottom of a micro tube. Add the enzyme solution whose acidity is adjusted to pH = 2 with HCL. Cover with toluene. Incubate 48–96 hours. Digestion is indicated by a strong red color in the solution.

Results: Pepsin was not present.

TRYPSIN.

Colored Fibrin Method: Stain fibrin 15–30 minutes in Anilin Blue. Wash with alkaline water (pH = 7.6) till all surplus stain is removed. Place a small piece of the blue fibrin in the bottom of the micro tubes and add the enzyme solution whose acidity is adjusted to pH = 7.6 with $Na_2 CO_3$. Cover with toluene. Incubate 48–96 hours. Digestion is indicated by a strong blue color in the solution.

Results: Trypsin was present in the fore gut, mid gut, and hind gut.

EREPSIN.

Modified Sorensen Method: Solution A: Add several drops of Brom Thymol Blue to a 4% peptone solution, and then sufficient KOH to give a blue color (pH = 7.6).

Solution B: Add several drops of Brom Thymol Blue to 40% Formalin and then sufficient 2% KOH to give a blue color. Add additional 2% KOH a drop at a time till when 1 cc. of this solution is mixed with 2 cc. of solution A, the resulting color remains blue.

Procedure: To solution A in the micro tubes, add the enzymes solution and toluene. Incubate 48–96 hours.

Then add a volume of solution B equal to one-half the volume of A in the micro tubes.

Digestion by erepsin with the liberation of amino acids is indicated by a greenish yellow to yellow color on the addition of solution B.

Results: Erepsin is present in the fore gut, mid gut, and hind gut.

Summary of Microchemical Analysis.

Enzyme	Found in contents of:
Amylase	Fore gut, mid gut, hind gut.
Maltase	Fore gut, mid gut.
Invertase	Fore gut, mid gut, hind gut.
Lactase	Absent.
Lipase	Fore gut, mid gut.
Pepsin	Absent.
Trypsin	Fore gut, mid gut, hind gut.
Erepsin	Fore gut, mid gut, hind gut.

General Conclusions.

In the tissue suspension experiments, no maltase could be detected in the salivary glands. Plateau states that the saliva can change starch to glucose, in which case maltase would necessarily be present. However, he took the positive Barreswil's test as an indication of the presence of glucose. This test is given by any reducing sugar, since Barreswil's and Fehling's solutions are practically identical. It was, without doubt, maltose and not glucose which gave the positive test.

The gastric secretion must be alkaline or at least only slightly acid since trypsin is the only enzyme present splitting complex proteins.

From the tissue tests, it appears that three enzymes, namely, maltase, invertase, and lipase are present in the cells of the fore gut. Plateau states that no enzymes are secreted by the fore gut, but that the digestive fluid from the gastric cœca rises into that portion of the gut and that digestion takes place there. It is also generally accepted, from morphological studies, that the fore gut does not secrete digestive juices. In these experiments, the contents of the fore gut were washed out thoroughly with distilled water. Any enzymes found there then, must be in the cells or the chitinous lining of the tract.

These enzymes therefore, must either have been formed by the cells of the fore gut, or absorbed by them from the digestive cavity. This cannot be settled by the evidence at hand. However, in the latter case, it would be expected that all the digestive enzymes found by the microchemical analysis in the fore gut, should also be found in the tissue preparation. This of course, is not necessarily so. Regardless of the origin of the

enzymes, we at least know that they are present in the fore gut and that most of the digestion takes place there.

Plateau's contention that the secretion from the gastric cœca rises into the fore gut is borne out by the fact that enzymes were found in the fore gut contents which could have been secreted only by the gastric cœca or the mid gut. As the mid gut secretes only small amounts, the gastric cœca would appear as the logical source of these enzymes.

The salivary glands and the gastric cœca are the most important sources of the digestive enzymes. The mid gut produces the same enzymes as the gastric cœca, but less abundantly. Its main function appears to be absorption rather than secretion.

The hind gut does not secrete digestive enzymes. Its main function appears to be the elimination of waste. Enzymes may be found in the contents of that portion nearest the mid gut, but are not demonstrable near the rectum. From this, it would appear that the enzymes are either reabsorbed or destroyed in the hind gut.

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PRINCIPLES OF PLANT TAXONOMY II.*

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THE EVOLUTION OF THE FLOWER.

The views and deductions presented below, as to the general nature of floral evolution, represent the results of twenty-five years of intensive study of the flower from the phylogenetic standpoint and are presented, for the most part, as the settled convictions of the writer, with the confidence that any one examining the evidence carefully will come to essentially the same conclusions. One of the striking differences between the sporophytes of the Bryophytes and those of the lowest types of Pteridophytes is the very determinate growth of the former and the indeterminate, repetitive growth of the latter. Ideal examples of such primitive, indeterminate systems are seen in *Lycopodium lucidulum*, *Botrychium virginianum*, and the typical tree ferns with a single, long-lived terminal bud. In the forward evolution of the more complex types of higher plants, some of the axes become determinate while other buds continue the indeterminate development. Determinate are axes of several types: first, a mere vegetative, special differentiation which ends in the permanent stopping of the growth of the bud, as in the small branches of *Lycopodium obscurum* and the sterile shoots and branches of most of the species of Equisetum; second, the development of a special organ from the bud, as a thorn or a tendril which differentiation usually brings about a permanent cessation of growth; third, the development of an abscission layer by which the terminal bud of the axis, or an entire branch is self-pruned; and fourth, the development of determinate, sporophyll-bearing axes or flowers in which the bud usually stops growing, much as in the first type, without any very special differentiation outside of the fact of sporophyll development. It is this last type of development that is the subject of the present paper.

In the flowerless, vascular plants, as for example, *Lycopodium lucidulum*, or *Osmunda cinnamomea*, the axis is continued

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indefinitely, giving rise to alternate zones of foliage leaves and sporophylls which in temperate regions usually have a rather definite relation to the seasons. From such indeterminate axes flowers evolve. A flower may be defined in the briefest way as a determinate sporophyll-bearing shoot, or a modification of such a shoot. Or in simpler words, a flower is a modified sporophyll-bearing shoot which has ceased growing permanently. It is important that this definition be thoroughly assimilated by those who wish to understand the evolution and phyletic classification of the higher plants.

A flower then has three fundamental characteristics, and these three peculiarities are present in the flowers of all living species. First, the most fundamental fact is the stopping of growth of the floral axis. If the flower is of a primitive type, i. e., not far removed from the indeterminate type of sporophyll-bearing axes, proliferation is a rather common occurrence. This proliferation is to be regarded as an atavistic or reversion phenomenon. The functional activity, through one cause or another, is not completely checked in cells of the terminal bud which continues a vegetative growth and sometimes a second or even third zone of sporophylls. Species in which proliferation can frequently be seen are *Equisetum fluviatile*, *Lycopodium obscurum*, *L. complanatum*, *Larix larix*, and among the higher types certain species of Rosa. The second characteristic of the flower, which is almost a consequence of the first, is the crowding of the sporophylls on the floral axis. This becomes especially striking in the higher species where internodes are developed between the foliage leaves or leaf whorls. The third characteristic is the specialization of the sporophylls as compared with the foliage leaves. This specialization of the sporophylls is not confined to flowers, but is often also very pronounced in the more highly specialized flowerless plants like *Osmunda cinnamomea* and *Onoclea sensibilis*.

Since the flower arises through a determinate growth of an axis in very primitive species, it follows that the most primitive flowers are solitary or isolated on the ends of leafy shoots and there is no abrupt transition between the shape and general character of the foliage leaves on the one hand and the sporophylls on the other. There is no flower cluster. Such conditions are seen in *Lycopodium annotinum*, the lower types of Equisetum, Araucaria, the carpellate cone of *Sequoia wash-*

ingtoniana, and in some higher types of flowers as *Magnolia foetida*. In Magnolia, although the flower, outside of its possession of a very primitive kind of perianth, represents a low type of strobilus, there is a distinct development of the peduncle which must be regarded as a considerable advancement. This development of a peduncle is probably partly due to the presence of a prominent internodal system. In primitive flowers, therefore, because of their position at the end of a free branch the symmetry is spiral and radially actinomorphic. In the main line of evolution, which leads to the living seed plants, the stem is a monopodial system, and sooner or later the floral expression is shifted from the terminal bud to axillary or lateral buds; or both terminal and axillary buds of the same branching system may become sporophyll-producing axes.

The lowest flowers, as would naturally follow in an evolution from indeterminate to determinate axes, usually have a large number of parts before the growth is discontinued. The process by which cessation of growth is brought about is developed very gradually when sporophyll production begins. Low types of flowers are, therefore, characterized by having large numbers of parts and these numbers are always indefinite. Such low types of flowers are to be seen in *Lycopodium annotinum*, *L. alopecuroides*, *Equisetum praealtum*, *Selaginella rupestris*, *Dioon edule*, *Araucaria imbricata*, *Agathis australis*, *Magnolia foetida*, *Myosurus minimus*, *Anemone cylindrica*, and *Rubus occidentalis*. In low types of flowers, when the species has a vegetative internodal system, there is sometimes a tendency to produce an internode between the andrecium and gynecium. Prominent internodal developments of this kind are found in *Michelia fuscata* and *Geum rivale*. The development of such internodes is probably due to the fact that the growing bud of the floral axis reverses its sex from the male to the female condition. In doing this it necessarily passes through a neutral state which produces the physiological condition of the vegetative shoot, and since in such a primitive flower the factors of determination act very slowly and slightly, it appears that under the conditions, the internode-producing factors are thrown into activity and a short internode is the result. But such flower-internodes are rare and apparently in most cases the factors of determination which are shortening the axis prevent any internodal growth even when the cells are passing through the neutral condition from maleness to femaleness.

The lower type of flower is usually called a strobilus or cone as distinguished from a higher "flower," but the transition is a very gradual one and the higher flowers have nothing characteristic in the floral development itself. One can only make clear distinctions on characters developed on the floral leaves themselves or other detailed structures. What are usually called "flowers" in our manuals and textbooks differ in the possession of closed megasporophylls or carpels with stigmas at their tips. But as stated, this is not a difference in flowers, but a difference in sporophylls. One can find just as fundamental differences in the various types of strobili. And even some of the flowerless plants have enclosed sporangia, like in the completely closed up leaflets forming the sporocarps of Marsilea or the partially enclosed leaflets of the sporophylls of Onoclea. The popular notion of a flower is something very showy, especially with bright colors. From such a viewpoint the cones of Norway Spruce, *Picea abies*, and the Longleaf Pine, *Pinus palustris*, become flowers, while ragweeds (Ambrosia) *Amaranthus blitoides*, and *Populus tremuloides* have no flowers.

Flowers were evolved in a number of entirely independent lines. In the Lepidophyta, there is still living a rather complete series of species ranging from the flowerless condition to a well specialized strobilus and even an inflorescence. In the Ptenophyta or fern phylum, no floral development seems to have appeared until the higher phyla, developed from this mother phylum, were evolved with heterospory and seeds. In the Calamophyta, represented among living plants by the genus, Equisetum, the determinate floral axis is also developed in the homosporous condition. Among seed plants, the lower Cycadophyta were also flowerless and this condition continues here and there even to the highest members of the phylum. The greater part of this fern-like phylum is fossil, but in the living genus Cycas, which is diecious, flowers appear only in connection with the male state. The carpellate plants, with the female sexual state, produce their megasporophylls on indeterminate axes in zones alternating with foliage leaves as in the ferns. In the Class Ginkgoæ, the one remaining species, *Ginkgo biloba*, also diecious, produces both its stamens and carpels on the indeterminate dwarf branches, alternating with zones of foliage leaves, thus showing the primitive flowerless condition. Some have interpreted the carpels and stamens

of Ginkgo as highly specialized strobili, but such a view seems entirely impossible. The carpels plainly show the vestige of a leaf blade, and the degree of evolutionary advancement does not agree at all with such a supposition. The carpel of Ginkgo is but the extreme of a reduction series as indicated in passing from Cycas revoluta through a succession of forms to Zamia. The stamen can easily be homologized with the stamen of the Bennettitales.

Among seed plants, therefore, many of the lowest species probably had no determinate axes, but a single indeterminate, terminal bud as in various tree ferns. In *Cycas revoluta*, the carpellate plant has no determinate buds, but the staminate plant produces determinate, staminate cones. In the higher Cycadaceæ both staminate and carpellate plants have indeterminate vegetative axes and determinate floral axes. Ginkgo is the highest species which has only indeterminate buds, since both the long and dwarf branches grow indefinitely. In Pinus the evolution of buds has developed as far in complexity as the higher lycopods and horsetails, having terminal indeterminate, vegetative buds on the long branches, determinate buds on the self-pruned dwarf branches, and determinate buds in the staminate and carpellate cones.

The living Strobilophyta all have flowers, ranging from very primitive types of strobili in Araucaria, Agathis, and Cunninghamia to such extreme reductions as the modified cones of Juniperus and Taxus, and the very highly specialized inflorescences of the Gneteæ or joint-firs.

The Anthophyta, as the name indicates, are also all flowering plants of the very highest types, the lowest representatives having flowers of indefinite numbers, and being spirally actinomorphic, like Magnolia and Echinodorus, not very far removed from the typical strobilus. Since the fossil record of the ancestors of the Anthophyta is practically a blank up to the present time, there is no way of telling at what stage of the evolution of the phylum flowers probably appeared. But the phylum appears to be an entirely independent line whose nearest known relatives are the flowerless, eusporangiate ferns. Taking the evidence from living representatives, it is clear that in some groups the flower condition was attained far down the scale in the homosporous stage of evolution, while in others the indeterminate axis was retained far beyond the heterosporous stage, even to a high degree of seed development.

The flowers of living plants can, therefore, be classified as: 1st, homosporous flowers, the most primitive type of strobili, as in Lycopodium, Equisetum, etc., 2nd, heterosporous, seedless flowers, as in Selaginella; 3d, heterosporous seed-bearing flowers with open carpels and without or with a very primitive development of the perianth, as in Cycadeæ, Coniferæ, and Gneteæ; 4th, heterosporous, seed-bearing flowers with closed carpels and with a well-developed perianth or vestige of one, or in a few cases with the perianth entirely obliterated.

The development of a perianth (sterilized modified sporophylls) is met with first as a rather definite structure in the highest Equisetaceæ, like Equisetum arvense, which has a small, calyx-like cup at the base of the cone, above the long peduncle. In some of the pines the carpellate cone shows two well-marked zones when young, as in *Pinus laricio* and other species. The lower zone of carpels remains small and does not develop seeds, while the upper carpels enlarge and the ovules develop into seeds. The Anthophyta all have bisporangiate flowers originally, with the stamens below, and the typical perianth must, therefore, be regarded as coming from modified, sterilized stamens or microporophylls. The lowest Cycadeæ (Bennettitales) also had bisporangiate flowers with the stamens below, but our living Coniferæ all passed promptly to the monosporangiate condition before the state of floral advancement was attained when a perianth might appear. We can safely say, then, that among living plants, the Anthophyta are the only ones which have a true perianth derived from the andrecium, and all living species at least have such flowers or flowers evolved from such a type.

The cause of the sterilization of the base of the strobilus or of the more highly developed Angiosperm flower is obscure. It has occurred to the writer that the cause may be partly due to a crowding in this part of the floral axis (lack of growth) and this crowding and the sterilization of sporophylls associated with it, may in turn be due to the conflict of activity and latency of the hereditary factors at this transition zone between the vegetative and reproductive parts of the axis, in which zone, owing to a rapidly changing gradient in the determinate axis, many vegetative hereditary factors are becoming latent while reproductive, sporophyll-producing factors are becoming active. A rapid physiological change, or crowding, would,

therefore, produce a conflict of reactions. Whatever the cause may be, the sterilization of the base of the flower with the display of color when it goes a little above the first steps of its development, i. e., the evolution of the perianth, is one of the most interesting among the many interesting phenomena of flower development.

The bisporangiate strobili of the heterosporous Selaginellas do not have their sporophylls arranged in such an invariable order as we find in the Anthophyta and Bennettitales. The megasporophylls may be at the base of the cone or more or less scattered along the floral axis or in alternate zones with the microsporophylls. As stated above, all the evidence available goes to show that the original heterosporous flowers were bisporangiate and that from this condition, from a very low evolutionary level to the very highest type of floral evolution as represented by the Compositales, there have been numerous lateral progressions, on every level and in almost every prominent group, to the monosporangiate condition, either resulting in one of the various types and degrees of moneciousness or in the more extreme diecious condition.

Not only do the primitive flowers represented by the various types of strobili, show prominently the progressive reduction of the floral axis and a crude development of a perianth, but other characteristics which appear in the higher forms are also evolved. The change from the green color of the primitive sporophyll is to be seen in the yellow cones of some Lycopods, in the chlorophylless cones of the four highest species of Equisetum, in the cones with special colors of some Cycads, and especially in the highly colored staminate and carpellate cones of some wind-pollinated conifers, especially in species of Picea, Larix, and Pinus, where the colors, including yellows, blues, violets, and reds, are usually most prominent at the time of pollination. In some of the most extremely specialized carpellate cones, as in some species of Chamaecyparis and Juniperus, the blue and purple colors are more especially produced in the mature fruiting stage.

Zygomorphy also shows itself to some degree, especially in various highly evolved pines, as *Pinus sabiniana*, *P. coulteri*, *P. radiata*, and *P. contorta*. Thus, as will appear from the more detailed account of floral development in the Angiosperms,

nearly all the fundamental specializations of the higher flowers are shown to a greater or less degree in the three preceding subkingdoms.

THE ANGIOSPERM FLOWER.

A typical flower of the more primitive type of Angiospermæ or Anthophyta may be defined as a hypogynous, spirally actinomorphic, bisporangiate flower with numerous parts indefinite in numbers, with the megasporophylls above and the microsporophylls below, and with an undifferentiated perianth theoretically derived from stamens or microsporophylls. All other types of living angiospermous flowers are plainly derived from this type. Of course, there are various other peculiarities in the angiosperm flower, as closed carpels forming an ovulary, a special stigma for pollination, greatly reduced gametophytes, very long pollentube, triple fusion, development of a xeniophyte, etc., but these are developments of or in the floral organs, rather than of the flower itself. The evolution of the flower may be reduced to five general, primary causes, as follows:

First. The progressive reduction of the floral axis through the earlier and earlier stopping of growth or determination of its terminal bud, leading to reduction of parts, coalescence or common development of parts which were once separate organs, and epigyny in which case the tip of the bud ceases its development before the floral organs have appeared and these are then developed from the further growth of the cortical region, the carpels in the extreme cases being merely more or less united vestigial structures capping the cavity of the ovulary, which is produced by the invagination of the cortical wall of the stem through growth. The ovules then develop from this wall rather than from the vestigial carpels themselves.

Second. The lateral expansion of the floral axis, either the part of the axis bearing the perianth and andrecium, the carpel-bearing axis remaining normal, giving rise to an hypogynous hypanthium, usually called a perigynous disk; or the carpel-bearing part of the floral axis alone expands as in Nelumbo; or the entire floral axis expands giving rise to cup-shaped receptacles as in Calycanthus; or the gynecium axis and the part of the axis bearing the perianth and andrecium both expand separately as in Fragaria. In the epigynous type of flower, the part of the cortex or axis bearing the perianth and stamens may

also develop, giving rise to the epigynous hypanthium, as in Cereus, Oenothera, etc. In the hypogynous type of hypanthium or perigyny, the hypanthium and outer carpellary parts may develop as a more or less common tissue, giving rise to the apple type of flower.

Third. The change of the flower from its primitive position as a terminal organ to a lateral or axillary position brings in a new relationship of one axis to another axis and often also a new up and down relation to gravity, resulting finally in bilateral or zygomorphic flowers. The bud develops more on one side than on the other, destroying the primitive symmetrical time-space relation of the leaf incepts, which originally gave rise to a spiral, actinomorphic symmetry of the shoot. How far the mere position of one axis on another, with its up and down and right and left relations, may be responsible for the evolution of zygomorphy is not evident. In the mosses, like Buxbaumia, for example, an erect radially symmetrical embryonic sporophyte, growing on an erect radially symmetrical gametophyte, finally develops a bilateral, more or less dorsiventral sporangium. There are, therefore, several fundamental causes combined in the adjustment and evolution of zygomorphic flowers and axes. Nevertheless, one can see even on a side-branch coming from an erect axis of a tree that such a branch is not radially symmetrical, but more or less bilateral or zygomorphic with an eccentric pith. Lateral branching systems are often decidedly persistently bilateral as in some Araucarians. The progressive development of zygomorphy from the original radial symmetry has a very decided influence on the evolution of the floral structures resulting in one-sided loss of parts and one-sided specializations or unions. Sometimes an isobilateral development comes about, although this is comparatively rare, and these isobilateral systems may also progress to zygomorphic systems. In rare cases, factors of irregular development are introduced which may transform a zygomorphic flower into a mature unsymmetrical type, as in Canna, which shows a complete series from spiral to cyclic actinomorphic condition, to zygomorphic structure, but finally becomes unsymmetrical in appearance through the irregular development of its staminodes and other organs.

Fourth. The relation of the time of sex determination to the ontogeny of the floral axis has been discussed somewhat

above. In the Angiosperms, the primitive, bisporangiate type of flower passes from the neutral, vegetative condition, with no sexual state present, to a male state or at least to a state that leads on to maleness in the andrecium and then reverses promptly and usually sharply to a female state or a state leading to femaleness in the gynecium, which state continues until growth of the flower bud ends. The original step in the evolution of the time of determination of the sexual state after it was transferred from the gametophyte of the homosporous plants to the sporophyte of the heterosporous plants is shown in such species as *Marsilea quadrifolia*, where the megasporangia and microsporangia arise side by side from the same tissue in the sorus. The next step was taken by such plants as Azolla, where only one kind of sporangia are produced in a sorus, but each sorus shows vestiges of the other sporangia, and both kinds of sori occur on the same leaf. The third step is represented by all normally developed, living, heterosporous species, where the time of sex determination is transferred back at least as far as to the incept of the sporophyll, giving rise to distinct microsporophylls and megasporophylls. The first arrangement in this type was probably a more or less intricate mixture of microsporophylls and megasporophylls as is still the case in some Selaginellas, and the second or higher type, characteristic of the Anthophyta, would come in with a more perfectly evolved, determinate axis in which the physiological gradient is progressively modified toward the tip and in which a zonal arrangement of sex-determination naturally follows, the male state coming first and the female state later, according to the peculiar hereditary constitution possessed by the Angiosperms and some other plants.

The first step in specialization of the sexual system was then to evolve hereditary systems in which some floral axes, in the normal environment, develop a male state and some a female state at the beginning of sporophyll production, which resulted in the monosporangiate type of flowers, and in case of primitive strobili apparently without vestiges of the opposite type of organs. But in the more complex, more highly evolved Angiosperms and some of the highest Gymnosperms, the Gneteæ, all sorts of gradations of vestigial stamens and carpels are produced. In the extreme condition, both monecious and diecious, no vestiges are developed under normal conditions, as in *Cannabis*

sativa. Such plants as the hemp, however, can easily be induced to develop bisporangiate flowers with the proper environment. By throwing the time of sex determination still further back in the ontogeny more extreme types of moneciousness are produced. In one type which is rather common staminate and carpellate flowers are produced in progressive zones, either the one or the other being developed first. In this case the inflorescence bud must undergo reversal and in passing from one sexual state to the other, it must necessarily pass through the neutral condition which may sometimes give rise to a zone of neutral tissue of some width. In this case a perfectly normal bisporangiate flower, a sex mosaic, or some monstrosity may develop, as would be expected. If the time of sex determination is shoved back into the seed or fertilized egg, a diecious sporophyte results. The flowers of such plants show the same kind of potentialities in the development of vestigial sporophylls and the bisporangiate condition as monecious species. In case a diecious species is closely related to a species with bisporangiate flowers and in case its hereditary constitution is such that the sexual states are not strongly fixed, then, if bisporangiate flowers are developed abnormally, the original sequence of stamens first and carpels last may be entirely lost and a stamen or a carpel may appear at any point or in any relation on the floral axis. A typical example of this kind is *Thalictrum dasycarpum*. It is evident, therefore, that vestigial sporophylls are due to two entirely different causes: First, the phylogenetic reduction of the floral axis, and second, the change in the time of sex determination.

For some reason not entirely clear to the writer, monosporangiateness is exceedingly rare in typical zygomorphic flowers, especially when they are far along in the line of zygomorphic specialization. With a moderate development of zygomorphy monosporaigiateness may be present as in the monecious *Aesculus glabra* and *Musa sapientum*. In the Compositales, monosporangiate flowers, either monecious or diecious, are rather common in the actinomorphic Helianthaceæ and Ambrosiaceæ, while they appear to be entirely absent in the Cichoriaceæ, in which all the flowers are ligulate and thus zygomorphic. The same general tendency may be seen in the zygomorphic Scitaminales, Orchidales, Scrophulariales and Lamiales. In the Fabaceæ also monosporangiate flowers occur

in the actinomorphic groups and are rare or absent in the higher zygomorphic groups.

It may be that in extreme cases of stamen reduction, pollination would become too precarious for the perpetuation of the species should monosporangiate conditions arise. Highly evolved zygomorphic species, on the other hand, frequently develop cleistogamy or parthenogenesis as in violets, bladderworts, and dandelions. But similar evolutions occur in actinomorphic series and in extreme wind-pollinated species as in Specularia, and in wheat.

Just as various specializations of the flower lead to self-pollination, so others result necessarily in cross-pollination. Among the most definite conditions leading to cross-pollination are dieciousness and proterandry and proterogyny.

Since monosporangiateness appears to be more abundant in the higher types of Angiosperm flowers than in the lower, and since these higher types are commonly reduced in size and often apetalous, and since wind-pollination is also a derived specialization, it happens that the flowers of wind-pollinated Angiosperms are usually though not always inconspicuous; while in the more primitive Coniferæ the large strobili may be very conspicuous, colored objects even though monecious and wind pollinated. In the higher types of conifers and joint-firs (Gneteæ), there is also a decided reduction of the flower as shown by such groups as Taxaceæ, and Juniprus when compared with the very primitive Araucariaceæ or some of the lower genera of Pinaceæ. When one looks into the matter, however, one finds large numbers of very minute and inconspicuous flowers among the higher insect pollinated species also.

Fifth. In the evolutionary progression of the flower from the primitive, green strobilus with only slightly modified sporophylls, there has occurred a great increase in the diversity of hereditary factors which give expression to minute characters in the floral parts. This complexity in the higher species shows itself in the development of various chemical contents, especially in color substances; in diversity of surface appearances; in appendages of various kinds; in peculiar shapes and forms, as specially developed crowns; in color patterns of almost endless variety, especially in the corolla, but by no means confined to it; in many types of stamens, pollen, and pollen-masses; in the special development of petal-like staminodes; and in the

diversity of nectar-producing surfaces, pits, spurs, disks, hairs and the like.

These five general types of evolutionary activities—shortening of the floral axis, expansion of the floral axis, zygomorphy, displacement of the time of sex determination and reversal, and development of the complexity of special morphological and physiological hereditary factors—have produced an almost endless diversity of floral form, structure, and quality, and have made the flower a very important organ for determining phyletic relationships. So far as fundamental types are concerned, all flowers may be reduced to eight morphological systems and can be represented by eight general diagrams, which with few modifications can be used to represent all the structures, and relations necessary for a proper study of floral evolution. These eight types of flowers, as indicated in the modification of the floral axis, are as follows:

1. Hypogynous, with no special distortion or expansion of the floral axis. Examples—Magnolia, Lilium, Geranium. Fig. 2.

2. Hypogynous with expanded gynecium axis. Example—Nelumbo. Fig. 4.

3. Perigynous, with free hypogynous hypanthium and normal gynecium axis. Examples—Geum, Rosa, Rhexia, Baptisia. Fig. 7.

4. Perigynous with the entire floral axis expanded continuously, bearing all the floral organs on a broad disk. Example—Calycanthus. Fig. 5.

5. Perigynous, with separately expanded gynecium receptacle and hypogynous hypanthium. Examples—Fragaria, Duchesnia. Fig. 6.

6. Perigynous with adnate hypanthium. Examples—Malus, Amelanchier. Fig. 8.

7. Epigynous, without hypanthium. Examples—Hypoxis, Cypripedium, Asarum, Helianthus. Fig. 9.

8. Epigynous with epigynous hypanthium. Examples—Euryale, Cereus, Fuchsia, Curcurbita. Fig. 10.

Of these eight types, Numbers 2, 4, and 5 are rare, and 6 is also restricted. The vast majority of flowers are developed upon the plans represented by Numbers 1, 3, 7 and 8.

It must be recognized that there are occasionally transitions between these types and in characterization of any species or representing it by the appropriate diagram it must be referred to the type to which it has the nearest affinity.

TERMINOLOGY.

The terminology of the flower is still far from satisfactory. Selecting the terms that appear to be the most suitable, the angiosperm flower may be described as follows:

- Flower
  - Sporophylls (Fertile or Sporebearing Organs)
    - Gynecium (Carpel set)
      - Carpel or Megasporophyll
        - Stigma
        - Style
        - Ovulary
          - 1 or more ovules (Modified megasporangia)
    - Andrecium (Stamen set)
      - Stamen or Microsporophyll
        - Anther
        - Filament
          - Mostly 2 or 4 Micro-sporangia (Pollen-sacks)
  - Perianth (Sterile Organs)
    - Corolla (Petal set)
      - Petal
    - Calyx (Sepal set)
      - Sepal

Some flowers have, of course, only a part of this complete set of floral organs. In extreme cases there may be only a single stamen or a single carpel.

Flowers are bisporangiate, monosporangiate, or in extreme cases completely sterile. If monosporangiate, then the flowers are staminate and carpellate and the plants either monecious or diecious. When the plants are diecious the individuals are either staminate or carpellate.

Flowers are (1) spiral or cyclic (special type of spiral);
(2) hypogynous, perigynous, or epigynous;
(3) symmetrical or rarely unsymmetrical.

If symmetrical, flowers are spirally symmetrical, or cyclically symmetrical. The symmetry is actinomorphic, radially symmetrical in two or more planes; isobilateral, symmetrical in two planes making different types of halves; or zygomorphic, with only one plane of symmetry.

If the flowers are cyclic, they may be dicyclic, tricyclic, tetracyclic, pentacyclic, etc.

The parts in a cycle may be dimerous, 2-parted; trimerous, 3-parted; tetramerous, 4-parted; pentamerous, 5-parted; hexamerous, 6-parted, etc.

Corollas are choripetalous or sympetalous, or the flower may be apetalous.

The calyx is chorisepalous or synsepalous, or the flower may be asepalous.

The flower may be entirely without a perianth or naked.

The gynecium may be apocarpous or syncarpous, simple or compound; and in respect to cavities, the ovulary may be unilocular, bilocular, trilocular, quadrilocular, quinquelocular, plurilocular, etc.

The stamens may be free, or synantherous, or if the filaments are united in various ways, monadelphous, diadelphous, triadelphous, etc.

OBSERVATIONS ON SPECIAL FLORAL PHENOMENA.

POLLINATION.—Primitive pollination was probably merely accidental, either on the ground or on the plant by means of wind, rain, gravity, or animals. From this unspecialized condition various types evolved, in the Gymnosperms mostly wind pollination, but to a small extent insects are also agents. In the Angiosperms the evolution was first to the undifferentiated type of insect pollination, which is the lowest type in the living species, and from this type in various lines the progress was to wind pollination (anemophily), which may arise even in the highest groups, (2) to water pollination (hydrophily), comparatively rare, (3) to specialized animal pollination (mostly entomophily), and (4) to various types of cleistogamous flowers and self-pollination. Cleistogamy has arisen from both the entomophilous and anemophilous conditions. The undifferentiated entomophilous flower usually has very complete pollination, while the highly specialized adaptations to insect pollination are often very inefficient, resulting only in a small percentage of pollinated stigmas, as for example, the common milkweed (*Asclepias syriaca*) in which the writer found less than one in eighty flowers pollinated in some localities in spite of the presence of many species of insects which visited them. Various types of self-pollination are also very efficient as for example the wheat and violet. Most of such evolutionary developments of the flower have no causal relation in advantage or utility. Some entomophilous species have self-pollination.

As a general rule, the lower types of flowers are necessarily large and conspicuous, while most of the very highly specialized types, whether petaliferous or apetalous, entomophilous, anemophilous, or hydrophilous, are small and inconspicuous. This inconspicuousness is, however, often compensated because of the massing together in large inflorescences, as for example the staminate catkins of *Populus deltoides*, the heads of *Bidens connata*, or the spikes of *Ibidium beckii*. Many flowers have nectar glands and are visited by insects for the nectar, as well as for pollen, but that there is no direct causal relation between the evolution of nectar glands and the advantage of insect visits to insure pollination is shown by the presence of prominent nectar glands on the leaves of such ferns like *Pteris aquilina*, which are visited by various insects. In certain species also, like the higher blue violets, the conspicuous flowers visited by insects are poor seed producers as compared with the cleistogamous flowers produced on the same individual. Such cases contradict completely the old utilitarian, selection hypothesis. The presence of nectar glands in flowers is then to be explained on the same basis as the presence of similar glands on the leaves and stems of both flowering and flowerless plants.

Double Flowers and Staminodes.—Since petals are sterilized stamens, any physiological factor evolved in the plant which changes the time or point of petal expression may cause other stamens to change to petals. Petal-like staminodes are common in various groups. Florists take advantage of this condition and by selecting such mutations have developed large numbers of so-called double flowers. In the composites the tendency to produce ligulate or zygomorphic corollas has given the so-called double composities. The tendency to sterilize the marginal flowers of other types as in Viburnum has given forms like the snowball. Such extreme mutations could of course not survive except through the care of man.

Decrease in the Number of Stamens.—In the vast majority of cases the evolution of the flower tends regularly toward the reduction of both stamens and carpels. If the flower is actinomorphic, the orthogenetic series pass from spirals of stamens of indefinite numbers to a definite condition of three or four cycles and then to two cycles, a common half-way station being the pentacyclic condition of the flower. This is followed by the elimination of the inner or outer cycle. But a

further reduction may occur leaving but two or one stamens. When zygomorphy appears, which is usually not until the flower has become at least partly cyclic, the two-cycled andrecium of a Monocotyl gives rise to the series, 6, 5, 3 (parts of 2 cycles), and then ends with either 2 or 1 stamens. If an unsymmetrical factor is introduced at the final stage, only a half functional stamen may remain in the flower. In the first transition from 6 to 5, the suppressed stamen may develop again here and there in the flower cluster, as in the banana (Musa). In the Dicotyls similar orthogenetic series are developed, from spiral to a two-cycle andrecium and then to one cycle. The higher Dicotyls are mostly tetracyclic and pentamerous. With the advent of zygomorphy the series passes from 5 stamens to 4 through all gradations of reduction and then to 2 and occasionally as in Salvia to 2 half stamens. And here also lost stamens may reappear in individual flowers as for example in Catalpa, which has two functional stamens and three prominent vestiges. By a careful search of a large number of flowers one can usually find among the normal type, here and there, flowers with 4 stamens, the two lateral vestiges being restored to the normal condition. Apparently such cases arise through some unusual physiological condition which prevents the inhibatory factors from bringing about a prompt determination.

Special Mutative Changes.—Species may change the usual plan of their flowers by a direct mutation, as a three spiral or three-parted condition to a two-parted one, or a five-parted set to a four-parted set or cycle. In such cases also, if the given species is near the original type, reversions are common in individual flowers, as in the common lilac (*Syringa vulgaris*) in which one can commonly find flowers with pentamerous corollas among the more typical tetramerous corollas which represent the derived type. Phenomena of this nature are very common all through the Anthophyta and must be properly understood before a correct disposition can be made of the phyletic relationship of the species involved.

Evolution of the Perianth.—In the more primitive Anthophyta, there is often little or no difference between the inner and outer sets of perianth segments. Sometimes there is but a single cycle which may be very brilliantly colored. From this undifferentiated condition, the series passes up on the one hand to differentiated cycles, a modified outer calyx often

green and of leaf-like texture, and an inner corolla, or on the other hand to a reduction or complete loss of one or both sets of the perianth segments. Usually some vestige remains, however, and completely naked angiosperm flowers are rare, except in the most extremely specialized species, where one meets with them occasionally. The evolution may also proceed, apparently, to the differentiated colored corolla and green calyx and then on from this condition to the elimination of one or both sets. Such eliminations are, of course, merely results of the evolutionary shortening of the floral axis. In the composites, loss of the corolla is comparatively rare, but few species have any prominent vestiges of the original calyx. In some the calyx is represented by a mere, slight ridge while in great numbers a new structure appears, the plumose pappus, which often evolves to a remarkable structure as in Tragopogon. In the lower type of flowers the perianth segments are entirely free, but as one goes up the evolutionary series there is a greater or less union of the segments, either in separate cycles or sometimes the inner and outer both together in a common structure. Sympetalous corollas also have adnate stamens abundantly. All such unions are to be ascribed to the shortening and modification of the bud of the floral axis, the cell differentiation process overtaking the cell development or cell lineage, the different processes of growth and hereditary expression being telescoped together, so to speak.

Evolution of the Gynecium.—The primitive gynecium consists of numerous free carpels, indefinite in number and spirally arranged. From this condition the evolution of the series is to a single cycle of free carpels, usually 3 in Monocotyls and 5 in Dicotyls. The next step is usually the union of these sets with as many cavities in the ovulary as carpels represented. But the evolution may continue without coalescence to a single carpel with one cavity. The usual course, however, is for the gynecium with a plurilocular cavity to be reduced to a single cavity, as a result of the continued earlier determination of the floral axis. Commonly part of the carpels become vestigial or disappear in this process. In Monocotyls, there are often only two stigmas left with a vestige of the third, as in the higher grasses, or only one, as in some Sparganiums. Such reduced gynecia then often look superficially like single carpels, although they are actually the culminations of originally com-

pound structures. In Dicotyls, an ovulary with five cavities is very frequently met at the half-way station up the evolutionary series. This may change directly to a unilocular ovulary with five stigmas, but commonly the stigmas are reduced to three and then to two, in either of which conditions the unilocular ovulary may evolve. Practically all the higher types of Anthophyta, both Monocotylæ and Dicotylæ, have such reduced, pluricarpous, unilocular gynecia, and it is only rarely that the unilocular condition is attained when the carpels are still numerous.

EVOLUTION OF THE INFLORESCENCE.

As stated above, primitive flowers are developed at the ends of ordinary leafy branches, the foliage leaves merging over into the sporophylls. A somewhat higher type appears in the shifting of the reproductive differentiations to the axillary buds of ordinary foliage leaves. From these two conditions, both of which may be present on the same plant, there is a gradual development of the flower cluster to the condition represented by the raceme, corymb, panicle, and cyme. These types are found in all degrees of development. By the introduction of branching factors which manifest themselves mainly in the reproductive shoots very complex panicles may be developed. On the other hand, complex flower clusters may evolve as the result of contraction or earlier determination of vegetative branching systems. Among the lower plants, flower clusters become evident in the Lycopods. *Lycopodium annotinum* represents the primitive condition with single or solitary strobili at the ends of leafy branches. *L. clavatum* usually has two cones on a specialized peduncle and this represents the simplest cluster possible. In *L. obscurum* there is also a beginning of clustering, although no special peduncle is developed. In *L. complanatum* the inflorescence is well evolved, because of repeated dichotomous branchings of the peduncle, commonly giving rise to eight or more cones. Among Conifers, a highly specialized staminate inflorescence is found in Taxodium. The numberous small staminate cones are borne in long, terminal, drooping, spike-like, branched panicles and the carpellate cones are usually also produced in small terminal clusters. In the Gneteæ, highly developed spike-like inflorescences are produced, which in the case of Tumboa and Ephedra simulate single

conifer strobili, and in Gnetum often look very much like ordinary aments.

Beginning then with a racemose or paniculate type of inflorescence, a simple or compound umbel, or a much-branched, flat-topped cyme or corymb represent some of the more specialized conditions. The first can be derived from a raceme by simply shortening the primary axis, leaving the pedicels of the individual flowers unchanged. The flat-topped cymes, like those of Sambucus and Viburnum, are extreme clusters in which a complex branching character has appeared and in which a high degree of differentiation is expressed. Such cymes and umbels may have the outer marginal flowers enlarged and sometimes sterilized as in *Viburnum opulus*, as stated above. Such sterile, conspicuous, marginal flowers are also present in the corymb of some Hydrangeas. By the addition of another hereditary factor, the sterile heredity may be expressed in the entire or nearly entire cluster, much the same as the tubular flowers of a Composite can all be transformed into ray flowers. Such a change has taken place in *Viburnum opulus*, giving rise to the well-known ornamental shrub called snowball.

If the main axis of a raceme remains unchanged, but the pedicels of the individual flowers are not developed, the result is a spike, and if the axis of such an inflorescence becomes fleshy we have a spadix. An ordinary spike which evolves a highly specialized slender, flexible axis is a catkin or ament. Panicles may also be reduced to spike like panicles. Among the most extreme inflorescences are heads, disks, and cyathia. These may arise from almost any of the preceding types by a shortening of all the axes in the inflorescence, which simply means a very early determinate growth of the system and consequently early process of special differentiation. Frequently in such inflorescences a considerable part of the stem below the flower-bearing part is involved in the shortening process, giving rise to involucres whose bracts are more or less modified leaves. If such plants are subjected to special manipulation, as severe cutting back at the proper time, the normally contracted part of the inflorescence axis will be somewhat elongated, in which case some of the involucral bracts will develop as normal leaves again. Such results can be brought about readily in *Helianthus annus* and *Arctium minus*, for example. A similar result follows in Helianthus if the plants are grown with a short daylight period.

The evolution of the inflorescence, therefore, follows in a general way the same lines as the flower itself. The extreme forms result from the earlier and earlier determination of the inflorescence buds, resulting in the massing together of the expressions of many hereditary factors. The differentiation thus overtakes the cell lineage or cell-division processes and the ontogenetic sequence is telescoped. In extreme inflorescences, highly colored bracts are often conspicuous features as in Poinsettia and other Euphorbias, in *Cynoxylon floridum*, and in various Aroids.

In the evolution of the more prompt determination of the inflorescence bud, the modification of a raceme, panicle, cyme, etc., may result in a reduction to a solitary flower. Such single flowers, as might be expected, are often large and conspicuous. They are never to be confused with the primitive type of solitary flowers, either terminal or axillary. Usually the character of the flower, its peduncle, the plant itself or a comparison with its near relatives will indicate whether such solitary flowers are of the primitive condition below the flower cluster stage or whether they have been derived by reduction from an inflorescence.

When there is an extreme condition of the inflorescence axis so that the differentiation processes overtake the cell development processes, the resulting cluster often simulates a single flower. So strikingly similar is the result that people in general who are not especially acquainted with floral structure almost invariably mistake such clusters as those of the composites for individual flowers. Such mimicry has no casual connection with any ecological selective agency as was formerly supposed, but the similarity of form is the result of a contracted life history of the inflorescence and flower shoots through which the factors become active in tissues and cells where formerly they were latent until the floral axis itself had been developed. As stated before, these are extreme cases of earlier determinations causing the differentiation process to overtake the ontogenetic development of the tissues.

As examples of such extreme developments the following may be mentioned: The cyathium of *Tithymalus corollata* develops five large petal-like bracts which makes the inflorescence look remarkably like an individual flower. Euphorbias have long ago lost their five petals, but petal factors are still

present, as well as a five spiral phyllotaxy which express themselves in the bracts developed from the mass of tissue developing the cyathium. *Parthenium integrifolium* usually has five marginal ligulate corollas corresponding to the five petals, etc., it has in its individual flowers. The same is true of the heads of *Ptiloria pauciflora*. Great numbers of such mimicking inflorescences, of course, do not have these numerical relations, since the expansion of the tissues of the disk rather tends, commonly, to increase the number of parts produced. The inflorescence of *Cynoxylon floridum* also simulates a single large flower because the four white bracts look superficially like petals. The inflorescence of the common fig, *Ficus carica*, is another extreme type in which the inflorescence develops as a hollow stem with the small flowers inside giving rise to a peculiar club-like structure. There is no mimicry of a flower, because the structure contains no bracts on the outside and because there are probably no petal factors left in the plant. Such extreme examples of inflorescences could be greatly multiplied, but these common types given are enough to indicate the general evolutionary trend.

INCORRECTNESS OF UTILITARIAN AND TELEOLOGICAL EXPLANATIONS.

A final word of criticism may be given in regard to a certain type of flower literature, voluminous in the past and still coming out in large quantities from both popular and supposedly scientific sources. With the advent of the doctrine of special design, of the utilitarian philosophy, and of the theory of the origin of species through natural selection, all types of minds could indulge in teleological abstractions and thus teleological literature in respect to the flower especially become both rampant and great. Both the popular and scientific literature on the flower of the immediate past are scientifically incorrect and often as ludicrous as the wildest flights of the "nature philosophers" of a hundred years ago, and both the wise and the foolish are still nourished with pabulum as follows: "Today we know that the manifold varieties of floral forms we see are mainly devises developed by the plant to secure the perpetuation of the species." "Plants have provided themselves." "Such flowers are rigid economists except in the matter of pollen, of which they are profligate spenders. Color, scent, and sweetness

are absent." "Honeysuckles and similar plants constrict their corolla so that only insects with long tongues can reach the sweets at its base." "To keep out the uninvited." "Each one of them (plants) has a purpose of its own from which nothing can turn it." "The plant lives only to produce its seeds." "After a while you will see why it needs so many more stamens than pistils." "The bright blossoms which it puts out are only to attract its messengers, the pollen carriers."

And so on, ad infinitum! Now the writer himself believes in a universal design in the creation, although a "special design," or a special utility, is far from his thoughts. He holds no anarchistic philosophy, scientific, political or otherwise. He has "communed" with plants poetically and scientifically since childhood, but never once has a plant told him that it desired to perpetuate its species, any more than the prairie fires he used to see long ago ever told him that they wanted to burn up everything in sight, although there is no doubt that they actually did do it. In fact, instead of imbibing in an unadulterated form the easy-going explanations of a utilitarian teleology, he was taught to believe, both from his contact with nature and from what to some appeared to be a rather stern catechism, that whether or no, "God works when and where and how He pleases." And this has always acted as a considerable check on his poetic flights of fancy. For what was the use to look for special designs and utilities if things go thus? They might be present or not.

But when all is said in a scientific way, flowers still have an esthetic and moral value that must not be overlooked; for this is just as fundamental and important as the scientific discovery of relationships and evolutions. It is not at all necessary, however, to present the moral and esthetic value of flowers in a false, utilitarian and telelogical dress.

EXPLANATION OF PLATE I.

Diagrams of the eight fundamental types of flowers. For particular information in respect to this method of representing floral diagrams, see "A General System of Floral Diagrams," Ohio Jour. Sci. 16:360, 1916. In representing spirals the actual pitch of the screw is not indicated except in the case of cyclic flowers, since this often requires considerable accurate measurement and complicated construction. For flowers with variable numbers an attempt is made to represent the most common type.

Fig. 1. Primitive homosporous flower corresponding in type to the primitive hypogynous type in the Anthophyta. Small cone from side branch of *Equisetum praealtum* Raf. The spirals are variable, as well as the sporophylls in each spiral.

Fig. 2. Hypogynous flower of *Scheuchzeria palustris* L., also of *Cabomba caroliniana* Gr. Hypogynous, actinomorphic, bisporangiate, pentacyclic, trimerous, choripetalous, apocarpous.

Fig. 3. Hypogynous flower of *Convallaria majalis* L. Same as Fig. 2, but syncarpous, and the perianth segments all united into one tube and the stamens united with the tube.

Fig. 4. Hypogynous flower with expanded gynecium axis of *Nelumbo lutea* (Willd.) Pers. Hypogynous, bisporangiate, mainly actinomorphic and spiral, with a general but distorted 3-spiral plan, apocarpous, and choripetalous with petal-like staminodes.

Fig. 5. Perigynous flower with the entire floral axis expanded continuously, bearing all the floral organs on a broad disk. *Calycanthus floridus* L. Flower on a spiral plan, apocarpous choripetalous, with no sharp distinction between sepals and petals, and with 6 vestigial stamens.

Fig. 6. Perigynous flower of *Fragaria chiloensis* (L.) Lam. with separately expanded gynecium receptacle and hypogynous hypanthium. Perigynous, bisporangiate, on the 5-spiral plan, actinomorphic, choripetalous.

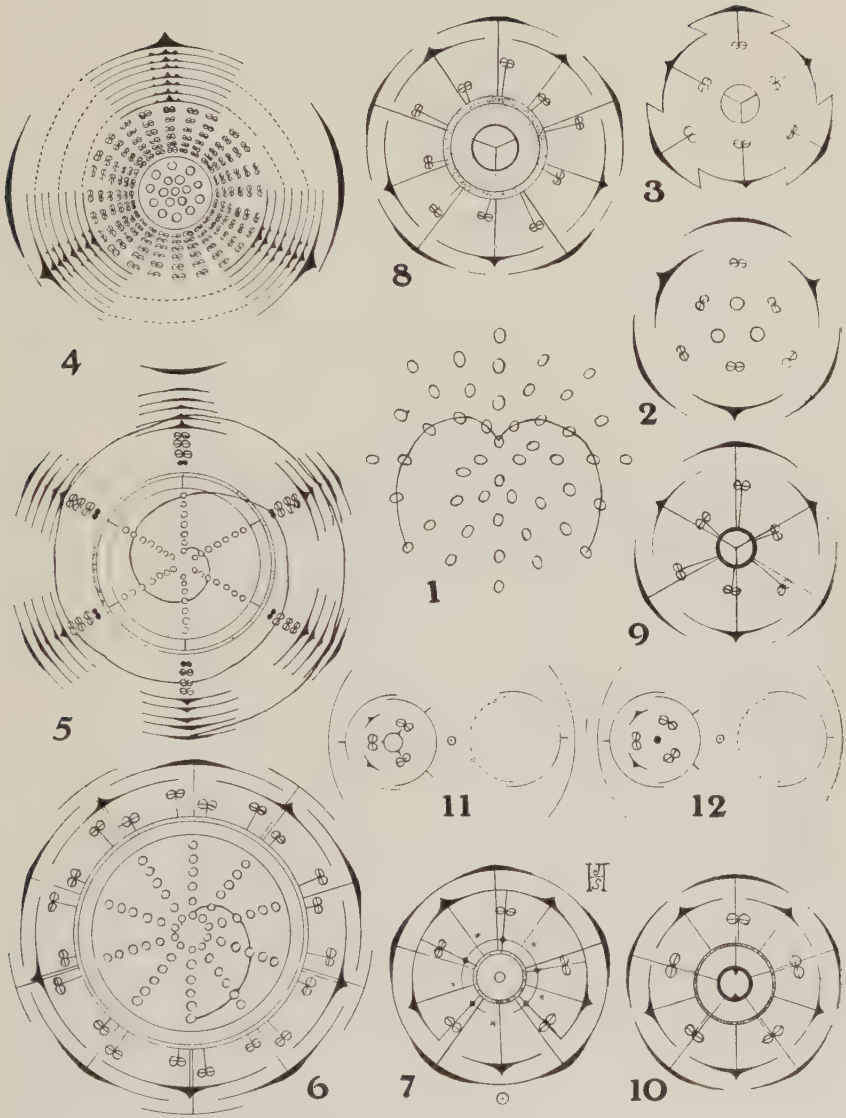
Fig. 7. Perigynous flower with free hypogynous hypanthium of *Petalostemon purpureum* (Vent) Rydb. Perigynous, bisporangiate, zygomorphic, tetracyclic by the loss of one cycle of stamens, pentamerous except the gynecium, which has one carpel, with four petals united, and with the stamen filaments united into an open tube which is united with the four united petals.

Fig. 8. Perigynous flower with adnate hypanthium of *Crataegus crus-galli* L. Perigynous, bisporangiate, actinomorphic, pentacyclic, choripetalous, pentamerous except the gynecium, which is trimerous and syncarpous.

Fig. 9. Epigynous flower without hypanthium of *Hypoxis hirsuta* (L.) Cov. Epigynous, bisporangiate, actinomorphic, pentacyclic, trimerous, chorpetalous, syncarpous with trilocular ovulary.

Fig. 10. Epigynous flower with epigynous hypanthium of *Ribes odoratum* Wendl. Epigynous, bisporangiate, actinomorphic, tetracyclic, choripetalous, pentamenous, except the gynecium, which is bicarpellate, syncarpous, and with a unilocular ovulary.

Figs. 11 and 12. Diagrams of sessile and stalked spikelets of *Andropogon furcatus* Muhl., the first with a reduced, hypogynous, bisporangiate flower and a lemma of a vestigial flower, the second with a hypogynous, monosporangiate flower, staminate through extreme reduction, and a vestigial lemma.



Diagrams of the types of flowers.

THE DIGESTIVE TRACT OF LONGISTIGMA CARYAE (HARRIS).*

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Introduction.

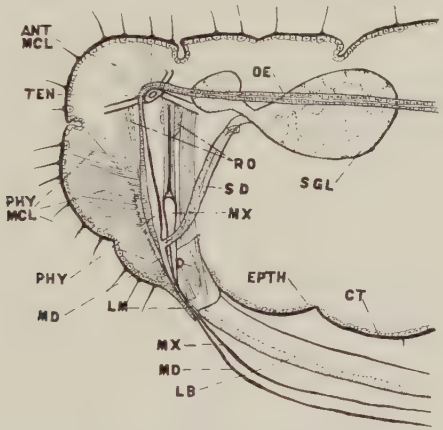
This work was undertaken because of the author's interest in Aphididæ, and the desire to become better acquainted with the internal structure. The Sycamore Aphid was chosen because of its large size and availability. All specimens studied were oviparous females containing eggs, collected between October 3rd and November 24th. Due to the unusually dry fall and the lateness of the season, it is doubtful whether even those earliest collected were obtaining much if any sap, which would possibly account for the stomach being closed for most of the distance in all cases. Specimens taken in early October showed signs of recent digestion in the epithelium of the mid-intestine, but those taken later had the cells more normal and showed practically no shedding of the cells. Even in late September the aphids were usually found with the mouth parts attached to the bark, unless they were on the under side of the twigs, ovipositing.

The Author is much indebted to Dr. C. H. Kennedy, under whom this work was carried on, for his suggestions and criticisms as the work progressed.

The digestive tract consists of a rather simple but slightly coiled tube, lying for the most part on the ventral wall of the abdomen (Plate I, Fig. 2). For a short distance the tube is complicated by the anterior end of the mid-intestine doubling back and forming a loop through the muscle wall of the posterior end of the mid-intestine and the anterior end of the hind-intestine (Plate I, Figs. 2 and 3). This loop enters through the muscle wall of the hind-intestine and enlarges (Plate I, Fig. 3 —Oe. V.) where the folds of the œsophageal valve return and join the stomach epithelium (Plate II, Fig. 1). Following the transition from fore- to mid-intestine, the stomach makes an

* Contribution No. 82 from the Department of Zoology and Entomology, Ohio State University.

S-shaped turn before enlarging greatly at the termination of the S into the open stomach until it becomes narrowed, except in a few cases, at the point of exit from being encased in the outer covering, formed by the posterior end of the mid-intestine (Plate I, Figs. 1, 2 and 3; Plate II, Figs. 2, 3 and 4.) In this double section the epithelium (Epth.) of the posterior end of the mid-intestine almost surrounds the anterior ensheathed portion of the stomach, although at no point can the fore end be observed to penetrate this epithelium (Plate I, Fig. 1; Plate II, Figs. 1 to 4). All of the coiled portion of the digestive tract is mid-intestine with the exception of the turn made by the anterior end of the hind-intestine at about the point where the œsophagus passes through its muscle layer.



Right half of head cut near median line, showing the mouthparts with some of the muscles, the salivary glands and duct.

The Gross Anatomy of the Canal.

The attachments consist of the invaginated body wall at the two ends, composing the fore and hind-intestines, with the supporting muscles.

The fore-intestine is comparatively simple in the aphid, lacking the crop and gizzard.

The mouth consists of the labium or lower lip which forms the rather long beak, the labrum or pointed upper lip, the stylet like mandibles and maxillæ that are operated by muscles in the head, and the tube connecting the pharynx with the beak, into which the salivary duct empties. (Text Figure of right half of head).

The pharynx is a sucking bulb supplied with numerous muscles from various parts of the head, but especially from in front. This pharynx relaxes into a rather horseshoe shape with the concave side in front. The pharynx extends nearly up to the tentorium apparently, and is flattened and wider in front of the tentorium, enlarging as it extends down towards the mouth. The pharynx lies behind the large brain, and between the two large nerves connecting the brain with the subœsophageal ganglion.

The œsophagus is a long, slender tube leading from the pharynx, over the tentorium to the œsophageal valve which lies under the muscles of the fore end of the hind-intestine, just before the mid- and hind-intestine come together. There is no indication of outpocketing along the œsophagus to form a crop or gizzard. (Plate I, Figure 2 and text figure of right side of head.)

The œsophageal valve is located just under the muscles at the anterior end of the hind-intestine, and is indicated by the enlargement in size just before the first turn, in the stomach which can be seen through the rather structureless hind-intestine. This valve is partly enclosed in the stomach epithelium which folds back around it, but which is not penetrated at any place by the tube. (Plate I, Figures 2 and 3.)

The mid-intestine is a coiled tube longer than the body, usually quite thick-walled, and lacking gastric cœca. Externally the mid-intestine, or stomach, has a mottled appearance when cleared in Carl's solution. For most of its length the stomach is closed or partly closed in the specimens the author examined, although this would not likely be the case in specimens taken when the food supply was abundant. In the portion where the stomach forms a double tube it is usually open in both sections, with the epithelium of the outer tube wrapped most of the way around the walls of the inner, making it appear at first glance that there is epithelium devloped on both sides of the muscle layer. Cross sections show very plainly that this outer epithelium is continuous with the outer tube epithelium, and that the inner tube has not punctured the latter. Food must pass the full length of the digestive tract to reach the anus. (Plate I, Fig. 2.)

The pyloric valve is not present, and the most evident mark of transition from the mid- to hind-intestine is the ending of the

large epithelial cells of the mid-intestine, and the beginning of the rather structureless and nearly transparent sack like hind-intestine, with its scattered prominent pavement-epithelium nuclei. This transition occurs a short distance before the œsophagus penetrates through the muscles of the hind-intestine.

The hind-intestine lacks the Malpighian tubules, and consists of a sack-like portion that is almost transparent for most of the distance, but connecting with the anus by the thick-walled rectum which has only a small opening through the center. (Plate I, Fig. 2.)

The intestinal valve consists of only a fold around the end of the sack-like hind-intestine, just before the beginning of the rectum. (Plate II, Fig. 9.)

The Histology of the Alimentary Canal.

**The "retortenformigen organen"* that Witlaczil explains and pictures from *Aphis pelargonii* are in many respects similar to those found in *Longistigma caryæ*. These organs lie in the sides of the head, one pair in front of the other, and outside of the muscles that retract the mandibles and maxillæ. In the sycamore aphid these are compressed laterally as shown by Whitlaczil, and the large distal end curves back as in *Aphis pelargonii*, but the proximal end tapers to the place it joins the mandibles and maxillæ. In explaining the origin of these organs Whitlaczil states that they develop from the rudiments of the mandibles and first maxillæ, which sink into the head, taking the skin with them, and are surrounded by the body wall. He goes on to explain that "The retort formed organs show in their fully developed condition, an outer layer of flattened cells which are continuous with the epidermis of the body and consist of a compact mass of large nucleated cells, which under this layer secrete a chitinous substance which hardens first on the point of the organ where it comes in contact with the air, and so forms the outgrowing bristle."

There is a small chitinized tube running up through this "retort shaped organ," largest where it joins the base of the mandibles and maxillæ. According to Whitlaczil, Mecznikow wrongly believed that the bristles were thrust out as in the

* Whitlaczil, Dr. Emanuel. Zur Anatomie der Aphiden, with three tables. Arbeiten aus dem zoologischen Institute der Universitat Wien, pp. 397–441, 1882.

Coccidæ, and in the resting stage rolled up in the "retort-shaped organs."

The cellular structure of the "retort-shaped organs" looks much like partly differentiated embryonic muscle in Longistigma caryæ, and the cells are not so large and distinct as pictured for *Aphis pelargonii*, those in the sycamore aphid being longer and narrower in proportion, and are easily distinguished in sections of the head.

The fore-intestine is histologically composed of the same parts throughout its length, but there is some variation in development of the parts. (Right half of head; Plate II, Figs. 1, 5.) The intima is thin and very delicate for most of the distance through the fore-intestine, which it lines throughout. The epithelium is thin, the cells are cuboid, usually clearly defined, the nuclei of medium size, oval to round and quite centrally located. Nucleus and cytoplasm granular, and nucleoli distinct. The basement membrane is delicate and structureless but can be distinguished. The longitudinal muscles are delicate, scattered strands of muscle at irregular intervals. The circular muscles form a rather continuous, fairly thick layer.

The œsophageal valve very clearly marks the transition from fore- to mid-intestine. The valve consists of a fold of epithelium, delicate cuticula and basement membrane from the œsophagus, which extends well into the small fore end of the mid-intestine and around the turn that occurs a short distance from the beginning of the stomach. The folds of epithelium then turn back to join the large stomach digestive epithelium cells at the point where the tube enlarges perceptibly at the end of the œsophagus. Histologically the parts coincide with the same structures in the œsophagus. (Plate II, Fig. 1.)

The mid-intestine is rather long in the aphid and very easily distinguished from the other parts of the tract. The peritrophic membrane, or some membranous tissue is found covering the inner surface of the digestive epithelium cells in the closed and partly closed portion of the stomach, but is not present, apparently in the open stomach except where no signs of recent digestion are in evidence. The digestive epithelium is composed of large, well defined cuboid cells with large oval to flattened nuclei, the nucleoli prominent and quite large, and the cytoplasm as well as the nucleus granular. In specimens taken early in October (Plate I, Fig. 1) the fore-end of the stomach showed

sloughing off of the digestive epithelium to a large extent, although some cells remained intact. In specimens taken late in November the fore-end of the mid-intestine was open, but little evidence of sloughing off of the cells was apparent. In the closed portion of the stomach (Plate II, Fig. 8) the cells are very large, and the intestine also contracted until there is little, if any, passage way left. The basement membrane is a rather thick, structureless membrane and easily distinguished. The circular muscles lie underneath and are delicate muscles in a discontinuous layer over the length of the mid-intestine. The longitudinal muscles are scattered, delicate strands at frequent but irregular intervals on the outside of the circular muscles.

The hind-intestine is sack-like and more than half as long as the aphid ending in a short, thick walled rectum. The intima is delicate, being thickest in the rectum, but hardly distinguishable in the quite structureless sack-like portion of the hind-intestine. The epithelium consists of flattened cells with indistinct nuclei and with the cell walls seldom distinguishable in the sack-like portion. The fold forming the intestinal valve, (Plate II, Fig. 9) and the rectum is composed of thick, cuboid cells with round to oval nuclei very distinct, and the cell walls clearly defined, nucleus and cytoplasm granular. There is only a slight indication of the six-sided rectum usually found in insects. The basement membrane is thin, structureless, not distinguishable as a rule until the rectum is reached. Here it is thin and structureless. The pavement epithelium is recognized by the large flattened nuclei scattered throughout the sack-like hind-intestine, being the most distinct structure in this rather structureless portion, except for the muscles surrounding it. The inner circular muscles form a discontinuous layer of delicate muscles throughout the length of the hind-intestine, and being most numerous around the rectum. The longitudinal muscles are delicate, scattered strands only. The outer circular muscles are present in strands, but do not appear so frequently as the inner circular muscles.

EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Longitudinal section through double portion of mid-intestine, showing epithelium wrapped around the inner portion of tract.

Fig. 2. Dorsal view of alimentary canal.

Fig. 3. Double section of intestine much enlarged, showing course of food.

Fig. 4. Cross-section of pharynx with muscles partly relxaed, showing the anterior at A.

PLATE II.

Fig. 1. Oesophageal valve with portion of oesophagus and hind-intestine, and the valve wrapped in the stomach epithelium.

Fig. 2. Cross-section of tube where double, just before emegrence at posterior end of double section. Shows epithelium wrapped around most of inner intestine, and muscles only connecting the folds in one place.

Fig. 3. Cross section through S-shaped portion of mid-intestine and hind-intestine, showing a layer of epithelium surrounding most of the inner folds of the tract.

Fig. 4. Longitudinal section showing emergence of anterior end of mid-intestine from near posterior end of same, where tract is double. Note epithelium pushed back by inner portion of intestine.

Fig. 5. Cross section of oesophagus much enlarged.

Figs. 6 and 7. Cross sections of open mid-intestine.

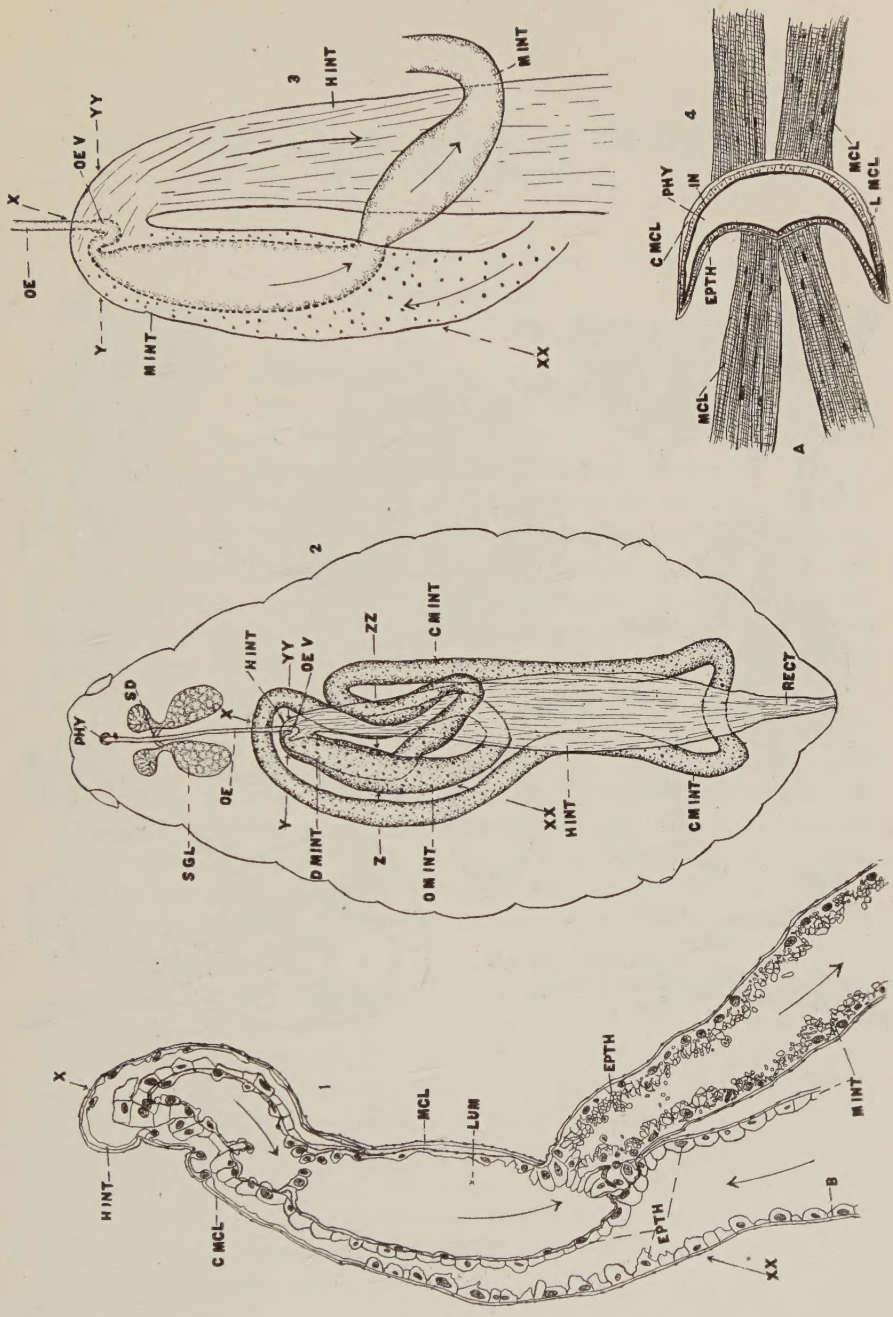
Fig. 8. Cross section of closed mid-intestine.

Fig. 9. Longitudinal section of posterior end of hind intestine showing end of sack-like portion, intestinal valve and rectum opening at anus.

Fig. 10. Salivary glands and duct, showing the cells that stain at different intensities.

EXPLANATION OF ABBREVIATIONS.

A, anterior.
AN, anus.
ANT MCL, antennal muscle.
B, basement membrane.
C MCL, circular muscle.
C M INT, closed mid-intestine.
D M INT, double mid-intestine.
EPTH, epithelium.
H INT, hind-intestine.
IN, intima.
INT, intestinal valve.
LB, labium.
LM, labrum.
L MCL, longitudinal muscle.
LUM, lumen.
MCL, muscle.
MD, mandible.
MX, maxilla.
OE, oesophagus.
OE V, oesophageal valve.
O M INT, open mid-intestine.
PHY- pharynx.
PHY MCL, pharyngeal muscles.
RECT, rectum.
RO, "retort-shaped organs."
SD, salivary duct.
S L, salivary gland.
TEN, tentorium.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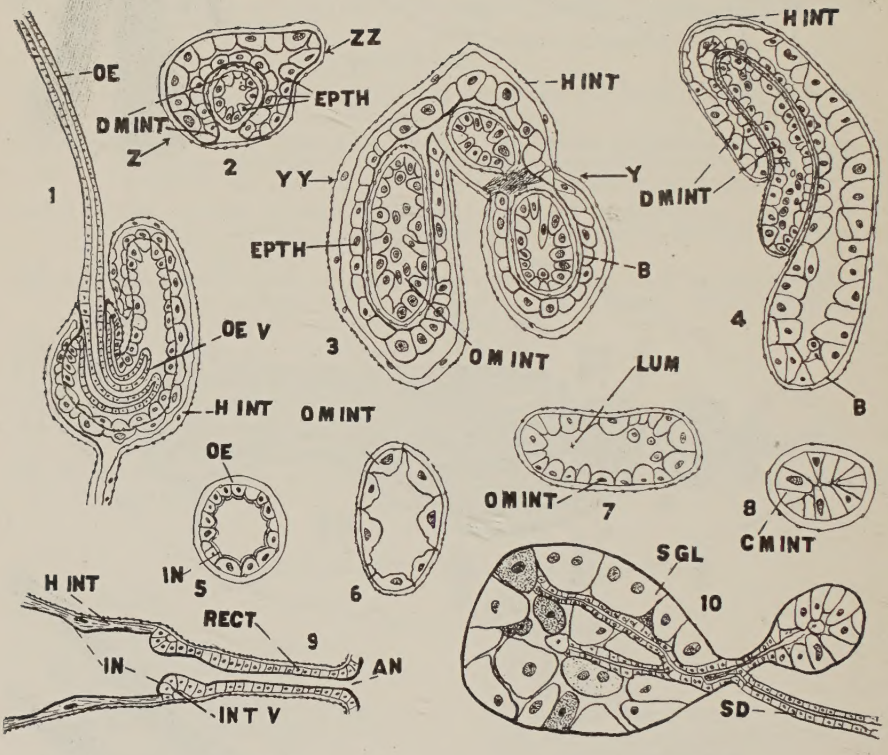
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INSECT FOOD HABIT RATIOS IN DEATH VALLEY AND VICINITY.

HARRY B. WEISS
New Brunswick, N. J.

In "North American Fauna," No. 7, pp. 235–268, 1893, there appears a "Report on a Small Collection of Insects Made During the Death Valley Expedition," by C. V. Riley, with supplementary papers by Williston, Uhler and Bruner. Some 557 species are listed from such localities as San Bernardino County, Death Valley, Panamint Valley, Panamint Mountains, Argus Mountains, Coso Valley and Owens Valley. As the records of the collection offered tabulation possibilities, the activities of the insects reported, were reduced to certain food habit types, based on the predominating larval habits of the families, and expressed as ratios.

These ratios should be considered only as tentative in view of the fact that the collection upon which they are based is not as complete as it might have been, this being admitted in the report. Nevertheless as all of the important orders of insects were represented, it was thought that the species might possibly constitute a representative sample and so in spite of evident imperfections, the tabulations were made as matter of interest.

According to published accounts, the vegetation of the entire area in which the insects were collected is scant and descriptions of the whole territory abound in such terms as patches or scattered sparse growths of pinon and juniper trees, poorly supplied with grass and water, alkali flats, salt beds, bare mountains, hot springs, cacti, sand, yucca, western juniper, small-nut pines, beds of dry lakes, cones of extinct volcanoes and heaps of pumice. From such statements it can be assumed that the vegetation over the entire area, although sparse, is of the same general type.

In accordance with their family food habits, the 557 species can be grouped as follows:

Number of species	557
Phytophagous	37 per cent
Saprophagous	20 per cent
Harpactophagous	25 per cent
Parasitic	14 per cent
Pollen feeders, misc. spp	4 per cent

Unfortunately there are no food habit ratios from a similar area with which the above figures can be compared to serve as a check. They are unlike the sets of ratios present in areas embodying different types of vegetation as noted in the Proceedings of the Biological Society of Washington, Vol. 38, pp. 1–4, Table I and appear to exhibit a degree of variation similar to those found in areas which have uniform types of vegetation. (Proc. Biol. Soc. Wash. Vol. 38, pp. 1–4, Table II). In view of this, it is assumed that the food habit ratios of Death Valley and vicinity afford additional evidence for the support of the suggestion advanced in previous papers*, that in relatively small areas each with a uniform type of vegetation, the ratios between the various types of food habits, based on the species present, vary in accordance with the type of vegetation, if the numerical ratios between the species and the factors tending to reduce or change their numbers are considered as constant.

* Ohio Jour. Sci. Vol. XXIV, No. 2, pp. 100–106; Ent. News, Vol. XXXV, pp. 362–364; Proc. Biol. Soc. Wash. Vol. 38, pp. 1–4.

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